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Illustrated Key to the Sections and Subsections and Brief General Circumscription of *Allium* subg. *Melanocrommyum*

By

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With 63 figures

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Summary

FRITSCH R. M. 2012. Illustrated key to the sections and subsections and brief general circumscription of *Allium* subg. *Melanocrommyum*. – Phyton (Horn, Austria) 52 (1): 1–37, with 63 figures.

Nomenclature, taxonomic history, and a concise description of main morphological and other traits of *Allium* subg. *Melanocrommyum* (comprising 169 species and subspecies) are presented. The illustrated key for the sections and subsections is accompanied by an actualized brief version of the conspectus published in 2010.

Zusammenfassung

FRITSCH R. M. 2012. Illustrated key to the sections and subsections and brief general circumscription of *Allium* subg. *Melanocrommyum*. [Illustrierter Bes-

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timmungsschlüssel der Sektionen und Subsektionen und kurze allgemeine Charakterisierung von *Allium* subg. *Melanocrommyum*.] – Phyton (Horn, Austria) 52 (1): 1–37, mit 63 Abbildungen.

Neben der Nomenklatur und taxonomischen Geschichte von *Allium* subg. *Melanocrommyum* (mit 169 Arten und Unterarten) wird eine kurze Übersicht der hauptsächlichen morphologischen und anderen Merkmale gegeben. Der illustrierte Bestimmungsschlüssel für die Sektionen und Subsektionen wird durch eine aktualisierte Kurzversion des 2010 publizierten Konspekts ergänzt.

1. Nomenclature

Allium L. subg. *Melanocrommyum* (WEBB & BERTHEL.) Rouy. Fl. France 12: 378 (1910), WENDELBO in Bot. Notiser 122: 27 (1969), *Allium* sect. *Melanocrommyum* WEBB & BERTHEL., Hist. Nat. Iles Canaries 3, 2 sectio 3: 347 (1848). – *Allium* sect. *Melamprason* F. HERMANN, Feddes Repert. 46: 58 (1939).

Type: *A. nigrum* L.

Moly MOENCH, Meth. 286 (1794), non MILL. (1754). Type: *M. speciosum* MOENCH (= *A. magicum* L.), *Allium* sect. (?) *Moly* (MOENCH) ENDL., Gen. Plant. 1: 147 (1836).

Ophioscorodon WALLR., Sched. Crit.: 129 (1822), p. p., quoad *Ophioscorodon magicum* (L.) WALLR.

Molium (G. DON) HAW., Philos. Mag. Ann. Chem. 1832: 284 (1832), sect. *Molium* G. DON ex KOCH, Syn. Deut. Schweizer Fl.: 714 (1837), p. p., quoad *Molium nigrum* (L.) HAW.; *Molium paucibulbosum* HAW.

Panstenum RAF., Fl. Tellur. 2: 20 (1837). Monotypic: *Panstenum monspessulanum* (GOUAN) RAF.

Canidia SALISB., Gen. Pl.: 92 (1866). Monotypic: *Canidia magica* (L.) SALISB.

2. Taxonomic History

Peculiar characters of *A. nigrum* s. l. were already recognized in the 18th century and initiated several authors to create new genera separating this and morphologically similar species. WEBB & BERTHELOT 1848 were the first having done this at sectional level. The initial description of *A.* sect. *Melanocrommyum* included solely *A. nigrum* and contained only anatomical characters of the ovarium (3 locules, per locule 3–10 horizontal or ascending ovules in central placenta-like position). However, REGEL 1875 found 2 ovules per locule for many species and included sect. *Melanocrommyum* and sect. *Kaloprason* K. KOCH (described in 1849) in sect. *Molium*. BOISSIER 1882 affiliated only *A. akaka* and similar species to sect. *Molium* and those species having 3–10 biseriate ovules per locule to sect. *Melanocrommyum* where he included many species from Asia Minor, Middle and Near East. Acceptance of this section at subgeneric level by ROUY 1910 has only nomenclatorial importance; it remained common practice to apply sectional classifications till past the first half of 20th century. For example, VVEDENSKY 1935 used a slightly "modernized" classification of REGEL 1875 with a widely accepted sect. *Molium* up to his last contribution of 1971 (VVEDENSKY & KOVALEVSKAYA 1971). A more comprehensive morphological characterization given by HERMANN 1939 (for the synonymous sect. *Melamprason*) remained generally ignored perhaps because it was mainly based on species occurring in Europe. Remarkable progress was presented by WENDELBO 1969 after having studied many species from Southwest Asia. He described several new sections and concluded that sect. *Melanocrommyum* jointly with these new sections and sect. *Kaloprason* constitute one somewhat heterogeneous taxonomic unit. WENDELBO regarded taxa remaining in sect. *Molium* in the strict sense to be much closer related to sect. *Briseis* (SALISB.) STEARN and to be separated by many characters from those belonging to the sections *Melanocrommyum* and *Kaloprason*. Therefore he accepted both as suprasectional groups at subgeneric level (for which the elder combination of ROUY and subg. *Amerallium* TRAUB, instead of subg. *Molium*, are the valid names). WENDELBO's morphological description of subg. *Melanocrommyum* mentioned the presence of single bulbs rarely bearing bulbils, all leaves are basally inserted and plane or canaliculate, their supraterranean sheath parts are not covering the scape, and the pedicels are ebracteolate. A similar morphological characterization but a different circumscription of subg. *Melanocrommyum* was presented by KAMELIN 1973 who subsumed WENDELBO's sections under sect. *Melanocrommyum*, and included the sections *Porphyroprason* EKBERG, *Microscordum* MAXIM., and *Briseis* as well as his newly described monotypic sections *Verticillata* KAMELIN and *Vvedenskya* KAMELIN. Nearly 20 years later, HANELT & al. 1992 presented another detailed classification of subg. *Melanocrommyum*. These authors accepted all sections of WENDELBO and sect. *Verticillata*, added the sections *Acmopetala* R. M. FRITSCH, *Compactoprason* R. M. FRITSCH (both segregates of sect. *Megaloprason* sensu lato), and *Miniprason* R. M. FRITSCH, but excluded the sections *Microscordum*, *Vvedenskya*, and *Briseis*. A detailed study of Central Asian species led KHASSANOV & FRITSCH 1994 to describe the sections *Acaule* R. M. FRITSCH, *Aroidea* F. O. KHASS. & R. M. FRITSCH, *Brevicaule* R. M. FRITSCH, and *Popovia* F. O. KHASS. & R. M. FRITSCH as members of subg. *Melanocrommyum*. Another classification of subg. *Melanocrommyum* by SEISUMS 1994 modified KAMELIN's 1973 proposal (excluding the sects. *Microscordum* and *Briseis* and including sect. *Nectaroscordum* (LINDL.) GREN. & GODR.), but one new section *Triptera* and five new subsections were never validly described.

Application of several molecular markers generally confirmed the circumscription of subg. *Melanocrommyum* proposed by HANELT & al. 1992. Analysis of ITS (internal transcribed spacer of nuclear ribosomal DNA) sequences corroborated the monophyly of subg. *Melanocrommyum* when sect. *Porphyroprason* is excluded (FRIESEN & al. 2006). This section as well as the sections *Vvedenskya*, *Caloscordum* (HERB.) BAKER, and *Anguinum* G. DON ex KOCH are the closest relatives of subg. *Melanocrommyum* and were also accepted at subgeneric level. Together they constitute the second, moderately advanced evolutionary lineage of the genus *Allium* (FRIESEN & al. 2006). Thus WENDELBO's 1969: 27 statement "*Melanocrommyum* is the most advanced of the subgenera" is not supported by molecular data.

From subsequent ITS analyses of multiple individuals of more than 100 species covering all existing infra-subgeneric taxonomic groups of subg. *Melanocrommyum* (GURUSHIDZE & al. 2008, 2010) followed i) that most classical sections are either para- or polyphyletic, ii) gene-flow among species (hybridization) is rare, iii) multiple rapid radiations occurred within different monophyletic groups of the subgenus, and iv) even separately evolving lineages within three morphologically clearly defined species were detected. An even more enlarged dataset (FRITSCH & al. 2010) allowed to recognize about 40 well separated molecular clades within the subgenus which demanded to newly describe the sections *Asteroprason* R. M. FRITSCH and *Procerallium* R. M. FRITSCH as well as the subsections *Humilicognata* R. M. FRITSCH, *Diffusoumbellata* R. M. FRITSCH, *Keratoprason* R. M. FRITSCH and *Pharmakoprason* R. M. FRITSCH. This publication also presented an updated conspectus of subg. *Melanocrommyum* affiliating 160 accepted species and subspecies and about 50 unclear or synonymous names to 20 sections and 22 subsections (the sections *Acanthoprason* and *Melanocrommyum* were only subdivided in alliances). During the last two years, several species were newly described; therefore an updated version of the conspectus (169 accepted species and subspecies; main amendments: reductions and inclusions of new species, no changes above species level) is given below.

3. Distribution

Members of this subgenus are naturally distributed from the Canary Islands to northwestern India (Kashmir), with a northern limit of distribution from Portugal and Spain, North of the Alps, Balkan Peninsula and Crimea to SW Siberia and western China, and a southern limit along the northwestern and northern coastal regions of Africa to northern Egypt, the Arabian Peninsula and Pakistan, with the centre of diversity in the eastern Mediterranean area, South-West and Central Asia.

4. Ecology

These taxa are adapted to different ecological habitats from sea level to alpine belt, but most species are typical xerophilous and heliophilous plants of dry steppes, semideserts or even sandy and gravelly deserts, rocky and stony slopes of arid mountains. Dry shrubs and forests, open semi-humid park-like associations, humid forests, meadows, and shady gorges are more rarely inhabited.

5. Morphological Outline

Earlier students of *Allium* morphologically described the groups we affiliate today to *A.* subg. *Melanocrommyum* at the actual level of personal knowledge at that time. Thus, a simple compilation of these formerly used characters cannot circumscribe the subgenus today. In the meantime, characters formerly considered as singular were found to occur also in other *Allium* subgenera, and some "missing" characters were also found among members of subg. *Melanocrommyum*. Therefore a rough general characterization is given below which, without claiming to be complete, tries to mention the many data gained during the last five decades.

The bulbs are ± depressed-ovate, rarely globose or sub-orbicular shaped, composed of 1–2 thick storage scales (the outer storage scale is generally much thicker than the inner one), tunics membranous to papery or leathery and/or fibrous but never reticulate. A rhizome is not visible. The tunics are composed of 2 sheath-like, early drying prophylls and the sheaths of the regular leaves of the last year(s). The majority of species form only one renewal bulb per year to replace the parental bulb, some species additionally 1–3 small, often ± stalked daughter bulbs, and only rather few species commonly form several larger and smaller renewal bulbs. Number and dimensions of all bulbs are species- or group-specific characters additionally influenced by the growth conditions.

Up to 200 roots per bulb may be present which are commonly not branched, annual hibernating (growing out in autumn and dying during or after anthesis next summer), about 1–2 mm in diameter, and penetrating the soil up to 40 cm deep (KAMENETSKY 1992). The anatomical structure is rather simple. Below the epidermis 6–8 layers of parenchymatic cortical cells are located, and in the center 1 stele is surrounded by in cross-section nearly isodiametric endodermis cells with strongly thickened outer walls ("O-type" of FRITSCH 1992a, anatomical marker for subg. *Melanocrommyum*). Contractile roots (anatomically characterized by radially dilatated, fusiform cortical cells; FRITSCH 1992a) move the bulbs (especially of seedlings) deeper into the soil.

One (rarely 2–3) scapes develop per bulb, above surface of soil most often terete but rarely really cylindrical, commonly long fusiform or long-conical (with the thinner part near top or base), surface smooth or sometimes lengthwise ribbed but never distinctly angular or alate. As most common in the genus *Allium*, the anatomical scape structure consists of one layer of epidermal cells, few to many layers of cortical cells (outer cells are chlorenchyma, the inner ones parenchyma; the number of cell layers is also changing along the scape), a tube-like region of sclerenchymatic tissue, and in the center parenchymatic tissue which may begin to dissolve very early. Vascular bundles are located among the central parenchyma, but most of them occur on rib-like protrusions along the outer limit of the sclerenchymatic tissue. These conditions cause rib-like structures generally visible on the scape surface of dried plants. At the cross section elliptical xylem vessels of scape vascular bundles are an anatomical marker of subg. *Melanocrommyum* (Fritsch 1993).

The growth form is similar to other bulbous *Allium* groups. The leaf sequence begins with one or two extremely thickened storage organs (cataphylls), continued by 1–2 elongated cataphylls without laminae enclosing the developing leaf bud (vernation is convolute) when growing through the soil, transitional to the foliage leaves. Normally only a lateral shoot of first order is developing in the axil of the uppermost leaf building the renewal bulb, more rarely several shoots are growing in the axils of additional leaves ("bulbs are dividing up"). Sometimes more than one lateral shoot from each leaf axil may develop and form side bulbs (Kruse 1992).

(1–)2–10(–15) leaves are present per bulb; they are composed of a basal subterranean sheath part and a more or less broad and long, supraterranean leaf lamina. In outermost position, 1–2 cataphylls (without laminae) are also visible above soil when the leaf bud is opening. These cataphylls are perishing prior to anthesis (but persist till anthesis for species of subsect. *Durovaginata*). The sheath part is not always tube-like, often there is a longitudinal slit commonly continuing the margins of the lamina up to the basal plate. Then the margins of consecutive leaves may be completely united one with the next (Kruse 1992). The lamina part is commonly (at least basally) channeled showing a great diversity of shapes from broadly ovate via lanceolate to linear. It is never carinate and commonly hooded at the tip. In sect. *Verticillata*, the lamina is divided into 3–12 thin and thread-like, parallel parts (not known from any other member of *Alliaceae* / *Amaryllidaceae* and even of order *Asparagales*). Anatomically, the laminae are characterized by epidermal cells much larger at the adaxial (upper) than the abaxial (lower) side (Fritsch 1988). The palisade mesophyll is slightly elongated in radial direction, with laticifers present in the transitional region to spongy mesophyll. Two rows of inversely orientated (xylem parts directed to the epidermis) vascular bundles are present. Always a pair of vascular bundles (one from upper and one from lower side) is connected as a path-like structure interchanging with tubular longitudinal holes stretching from base to tip area. This special configuration (an anatomical marker of subg. *Melanocrommyum*) develops by repeated bifurcations of nearly all vascular bundles beginning in the sheath part and continuing till the middle part of lamina; the descendent daughter bundles (with torsion by 180 degrees) construct the adaxial row (FRITSCH 1992c, "type F")

The spathe is commonly persistent, only short-beaked, prior to anthesis longitudinally splitting (often not completely to the base) into 2 to several deflexing segments, during and after anthesis membrane-like scarious (only *A. aroides* owns a permanent flat beak of leaf-like structure) and whitish to yellowish-brown with brown to purple nerves.

The inflorescences are cymose pseudoumbels composed of several helicoid or scorpioid cymes, they are many-flowered (20–50 flowers in sect. *Brevicaule*) up to extremely rich-flowered (more than 3000 in sect. *Compactoprason*). The shape is narrowly fasciculate to spherical (all intermediate shapes are possible) and is often changing from initially small and contracted to loose and broader or spherical shape during the course of anthesis. Only *A. regelii* may regularly bear two to five superposed inflorescence parts lifted by short scape pieces and basally enclosed by extra spathes. First flowers open preferably in the median region or are accidentally distributed over the whole upper two-thirds of the surface, and the last flowers (commonly with longer pedicels) open mostly near the base. After seed ripening, dry inflorescences may be decomposing (in sections *Thaumasioprason* and *Popovia*) or may roll (together with the adhering upper part of scape) over the soil blown by the wind ("tumble-weeds"), but most often they remain standing till autumn. The receptacle is semiglobose to nearly globose.

The pedicels are ebracteolate, of sub-equal to very unequal length, more or less elongating during and after anthesis (sometimes by 3–10 times in sect. *Regeloprason*), straight or slightly upwards (rarely downwards) bent, smooth to coarse, glossy to dull, whitish to green, often brown to purple flushed and then darker towards the base, more or less stiff and elastically wire-like, cylindrical or slightly angular with (sometimes thickened) conical basal end and a short-conical (rarely bubble-like) thickening below the flower

Most flowers are bowl-shaped to flat funnel-shaped and more or less star-like with tepals connected only near the very base, less often broadly to narrowly campanulate or long funnel-shaped, rarely more or less triangular with the outer tepals more spreading than the inner ones. The flowers of many species emit a faint honey-like scent, others a strong (not always appreciable) one.

Generally six tepals are present. They are extremely variable in dimensions (4–18 mm long, basally 1–4, near middle up to 6 mm wide) and shape but always longer than wide and commonly inner tepals wider than outer ones. Their shape varies from broad ovate or obovate to narrow linear or triangular and is often somewhat changing during the course of anthesis of a single flower (but in sect. *Stellata* the tepals of the last opening flowers may be by 1/3 shorter than those of the first flowers of the same inflorescence); the position is initially stellate or obliquely forward directed, sometimes deflexed or recurved near the basis. The tip of tepals is often longitudinally plicate, spoon-shaped or claw-like inflexed; the median vein is commonly darker and thicker than the lamina, sometimes broader near the middle of tepals or prominent at the outer side, commonly ending in the tip or slightly recurrent, rarely ending before tip. The margins are mostly smooth, rarely more or less toothed; near base they are mostly 0.3 to 1 mm long connate (often also united with filaments), rarely completely free or basally united up to 2/5 of their length (sect. *Regeloprason*). Tepal colors are very diverse, all kinds of conspicuous or inconspicuous tones of white to pink (sometimes with silvery shine), purple, dark-purple, and violet, or yellowish and brown may occur, rarely intermixed with green, but never truly blue; with the median vein commonly darker or green to brown, rarely inconspicuous in color and shape.

After anthesis the tepal shape is rarely unchanged, more often crumbled, irregularly to spirally contorted, often deflexed, sometimes convolute; texture most often becoming paper-like to parchment-like stiff, sometimes prickly (when the margins are convolute or the median vein becomes stiff; sects. *Acanthoprason* and *Asteroprason*), color commonly fading or becoming brownish.

Six filaments are always present. They are patent, rarely connivent, basally united with each other (commonly for 1–2 mm but much longer in sect. *Regeloprason*) and often also united with the tepals, basally triangularly, rarely quadrangularly, widened, sometimes (but then often only the inner filaments) with two (as rare exception four) triangular, rounded, or shoulder-like, sometimes very short tooth-like appendages. Above base the filaments are subulate, long-triangular, or long-ovate, commonly more or less fleshy, surface mostly smooth, very rarely hairy (sect. *Acmopetala*), from 1/4 up to two times as long as tepals, inner filaments often broader and/or shorter than outer ones; color extremely diverse from truly white or yellowish up to blackish-purple and dark-brown, dark colors often fading towards filament base, filament tip often becoming darker towards end of anthesis, sometimes (sect. *Melanocrommyum*) only transversally restricted zones are colored.

The anthers are ovate to oblong, rarely nearly linear, 1.5–3 mm long, 0.7–1.5 mm wide; color in diverse shades of yellowish or greyish white up to golden or greenish yellow, or brown, violet, and blackish-purple.

Pollen grains are shed as monads, they are whitish, greyish, or greenish yellow, rarely with reddish tones or brown. Detailed analyses are available only for a minority of species reporting pollen grains 26–37 µm long (equatorial axis E), 13–22 µm wide (polar axis P), form peroblate to suboblate (mean of P/E ratio 0.46–0.63), and in polar view boat-shaped. Small convex sculpture elements (“supratectal muri”) on the surface are more or less irregularely arranged and short (rugulate to microrugulate pattern, sometimes muri very shallow) with perforations of variable diameter in between, rarely long and parallel (transitions to striate condition). Only one long and narrow aperture (“sulcus”) is stretching over the distal pole (mono-anasulcate and heteropolar pollen grains). In general, the pollen grains are somewhat narrower than those of other *Allium* subgenera (NESHATI & al. 2009, and elder publications discussed therein).

The ovary is composed of three connate carpels with internal septal nectaries at the place of suture. The ovaries are mostly ovate to flat-globular, rarely obconical or pear-shaped, generally with six longitudinal furrows, three along the suture and three (sometimes very narrow) ones along the median veins of the carpels. The diameter of the ovary increases in the lower half of the ovary, or near the base first decreasing then increasing (“stipitate ovaries”), upper half most often six-grooved semiglobose with a more or less pronounced central depression; dimensions in full anthesis about 2–4 mm long and 3–4 mm in diameter. Sometimes the tip bears six radially or obliquely outwards directed outgrowths (“hornlets”, *A. olivieri, A. hexaceras, A. sarawschanicum*). The epidermal cells are radially elongated and have also slightly thickened inner periclinal walls (FRITSCH & KRUSE 1990); the outer periclinal walls may be slightly convex (“glossy ovaries”) or strongly convex, tuberculate, or papillous (“coarse ovaries”); the color is generally green, often partly or during a certain period purple flushed, as exception the epidermis may be colorless (*A. elburzense*) or more or less completely greenish black to purplish black when the flower is in full anthesis (many species of sect. *Melanocrommyum*). The nectaries are commonly located only in the lower half of the ovaries and excrete through downwards bent excretory tubes ending still below the bottoms of the locules in the angle between ovary and tepals as pit or slit, rarely somewhat higher in a tangentially widened pocket (sects. *Decipientia* and *Longibidentata*). Several sections show a specific shape of nectaries (FRITSCH 1992b, GURUSHIDZE & al. 2008). The ovule number per locule ranges from 2 (sect. *Compactoprason*) to 24 (*A. insufficiens*; FILIMONOVA 1970), with a mean of 4.7 (HANELT 1992). This number varies among locules and among flowers; most common 4–7 ovules occur per locule and develop into 2–4 seeds.

The gynobasic style is basally united with the ovary emerging from its tip, initially (sometimes shortly) conical, later subulate or filiform and mostly protruding from flower; whitish, sometimes finally pink to purple like the filaments. Stigma commonly punctiform, in full anthesis often slightly capitate, or rarely slightly tripartite, whitish.

The ovary develops into a loculicidal dry capsule opening along the dorsal furrow of the locules building three concave valves. The trigonous unripe capsules are about ovate, obovate, pear-shaped, or subglobose. The ovate to obovate, sub-orbicular or sometimes heart-shaped valves often develop raised wrinkles when drying out. Their surface is coarse and dull, rarely more or less smooth and glossy, variably greenish- or yellowish-brown. Mostly ripe capsules open widely with seeds falling out when the infructescences are shaken by the wind or by passing animals, or are tumbling over the soil; rarely (sect. *Compactoprason*) capsules open with a narrow slit and drop down from the pedicels when ripe.

The seed shape is very variable, strongly influenced by the dimensions of the developing capsules, especially the space available in the locules, and the number of seeds developing per locule. Mostly the seeds are flattened with convex or concave sides, the shape is ovate or drop-like, more or less pointed and irregularly shrivelled at the tip where the ripe seeds dropped from the placenta, angled, rarely sub-globular, with net-like or ledge-like, raised wrinkles, commonly slightly lustrous (rarely dull) black, as exception brown (sometimes in *A. aroides, A. verticillatum*). Shape, dimensions, and surface sculptures visible under a hand-lens may vary remarkably among accessions of the same taxon as well as among seed samples harvested in different years. The range of dimensions measured were 2–5 mm long, 2–4.5 mm wide, and 1–2.5 mm thick (FRITSCH, unpubl. results). Probably taxonomically relevant differences will be found when large seed samples can be compared. Measuring the thousand-kernel-weight (TKW) in a small random sample (HANELT 1992, 27 species) resulted in the mean of 4.84 ± 1,29 g (range 1.12–8.81 g) with the exception of 0.86 ± 0.05 g in *A. verticillatum* and generally more than 8 g in *A. giganteum, A. macleanii,* and *A. stipitatum*. These are the highest TKW in the genus, solely some groups of subg. *Amerallium* showed also TKW measures of 5 g and more.

Contrary to this morphological variation, the principal shape and sculpturing of testa cells investigated under a scanning electron microscope are rather uniform (FRITSCH & al. 2006). The periclinal walls are convex with several large prominent verrucae (with the exception of *A. aroides* and *A. verticillatum*). The areas between the verrucae may bear larger or smaller granules which may cover also the basal parts or even the whole prominent sculptures. The anticlinal walls are undulated with different amplitudes and different wavelengths; S- like, U-like and Omega-like undulations and also transitions between these types occurred. However, this sculpturing was generally very plastic, and species-specific as well as section-specific patterns could not be ascertained (FRITSCH & al. 2006). Only *A. aroides* (flat, densely granulose periclinal walls without verrucae, anticlinal walls straight or slightly bent without any true undulation) and *A. verticillatum* (periclinal walls sometimes warped and without verrucae, Omega-like undulation with extremely low amplitude and extremely short wavelength) showed species-specific patterns.

6. Other Traits

The base number of chromosomes is generally x = 8 (but x = 9 in *A. karataviense*, x = 10 in sect. *Decipientia*). Most species are diploids (sometimes with accessory chromosomes), in some species also tetraploids were found, but higher ploidy levels need verification. Concluding from diverse literature sources, several species show apparently varying karyotypes, but chromosome measurements of 23 species from Central Asia (FRITSCH & ASTANOVA 1998) showed rather uniform karyotypes without any clear species or section specific characteristics.

Life form and annual cycle. All species are perennial bulb geophytes with an ephemeroidal growth rhythm (HANELT & al. 1992), summer to winter dormancy, late spring to high summer flowering, and complete withering of leaves before spathe opening (PISTRICK 1992, KAMENETSKY 1992). Assimilating (supraterranean) organs are only visible for a few months, beginning with leaf sprouting in February to March, pre-flowering in April, anthesis in April to June, fruiting June to July. Leaf differentiation of the sprout of the following year (April till June) and inflorescence differentiation (August till October) is continuing during summer dormancy over a period of 4–6 months (KAMENETSKY 1992, 1996). Daughter bulbs develop along the margin of the basal plate, and renewal bulb and flower scape near the base of the inner storage scale (YUR'EVA & KOKOREVA 1992). Induction of scape and inflorescence differentiation takes place at relative high temperatures (KAMENETSKY & RABINOVICH 2002), but species from temperate and cool subtropical regions need several weeks of cool temperature to induce complete development of flower scape and inflorescence to anthesis (KAMENETSKY & FRITSCH 2002).

As far as investigated, seeds need a long period with low temperatures prior to germination (SPECHT & KELLER 1997). All investigated members of subg. *Melanocrommyum* showed epigeal germination with seedlings of the *A. karataviense*-type (DRUSELMANN 1992). During the juvenile stage, which lasts several years, the apical meristem produces only leaves, and the leaf form changes from the thread-like cotyledon to the species-specific final form and leaf number (KAMENETSKY & FRITSCH 2002).

Chemical characters. Fructose-based polysaccharides (10–90 % of the dry mass), saccharose, and reducing sugars (but no starch!) constitute the main reserve compounds in the bulbs (Fritsch 2005). Gluco-fructanes and other carbohydrates are also present in other parts of the plant (Khodzhaeva & al. 1998). Also different steroid saponins (Vollerner & al. 1991, Sokolova & al. 1993, Sokolov 1994), remarkable levels of flavonoids, alkaloids, and phenolic compounds (Sokolov 1994) are present in all plant parts and contribute to specific qualities of *Allium* plants. Several vitamins were reported to be present in the common onion (Keusgen 2002) and some also occur in species of other taxonomic groups (Sokolov 1994). The well-known strong taste and odor of the common onion, of garlic and of other consumed species is caused by different cysteine sulphoxides. These compounds disintegrate enzymatically into strong-smelling and hot-tasting sulphur compounds when cells are destroyed in any way. Cysteine-sulphoxides occur in the bulbs of members of subg. *Melanocrommyum* only exceptionally in high (0.5–0.63 % of fresh weight) but mostly in low (<0.2 %) to very low (<0.01 %) concentrations with dominating methiin, sometimes alliin, isoalliin, and low amounts of propiin or butiin, generally in concentrations changing from one species to another (Fritsch & Keusgen 2006; Keusgen & al. 2008). Therefore many species are nearly odorless. Some strong-smelling species contain other cysteine-sulphoxides: *A. suworowii* contains marasmin (Kusterer & al. 2011), and *A. stipitatum* and *A. altissimum* contain marasmin plus a pyridine cysteine-sulphoxide (Kusterer & al. 2010, 2011). The remarkable use of *A. stipitatum* as analgesic in Iran (Abbasi & al. 2008) is probably caused by this pyridine cysteine-sulphoxide (Kusterer & Keusgen 2009).

Bioactive compounds. Cheshmedzhiev & Karova 1990 did not find antibiotic activity in some species of sect. *Melanocrommyum* against bacteria and yeast. Jedelská & Keusgen 2008 confirmed lack of activity in several other species against Gram-negative bacteria, but reported considerable antibiotic activity of *A. rosenorum* against Gram-positive bacteria and expected, that extracts of many species are active against fungi. They reported high radical scavanger activity (higher than that found in garlic) for species of subg. *Melanocrommyum* containing a dithiodipyrrole cysteine-sulphoxide. The latter substance causes red color of wounded plant tissue and tissue exsudates, which is used as a characteristic of *Allium* leaves collected in the wild and used for dishes highly esteemed for tonic properties (Keusgen & al. 2006).

Proteins and nucleic acids. Serological affinities are much more pronounced to some rhizomatous sections and subg. *Amerallium* than to advanced groups of subg. *Rhizirideum* and subg. *Allium* (Hanelt & al. 1992). A strongly unreduced, salt-soluble seed storage protein with molecular weight of 65000–70000 was found in subg. *Melanocrommyum* only (Maass 1992).

The first molecular studies devoted to subg. *Melanocrommyum* (earlier studies focused mainly on the infrageneric relationships in *Allium*) were presented by Friesen & al. 1997 who applied genomic in situ hybridization (GISH) and random amplified polymorphic DNA (RAPD) markers to ornamental species. These authors confirmed hybrid origin of some but not of all cultivars declared to be hybrids, and presented evidence that cultivars of *A. hollandicum* are no hybrids and species like *A. macleanii* (including *A. elatum*) and *A. stipitatum* (including *A. hirtifolium*) must be accepted in a broad sense. Sequence analysis of the ITS region by Dubouzet & Shinoda 1998 used an extremely poor material sample design, and most infra-subgeneric relations and non-relations they postulated were abandoned by later comprehensive studies. Mes & al. 1999 used polymerase chain reaction amplified restriction fragments (PCR-RFLP) of noncoding regions of chloroplast DNA for a phylogenetic analysis in a wider taxon range. They found severe incongruence of morphology and chloroplast data and hypothesized a high level of interspecific gene flow within subg. *Melanocrommyum*. However, later ITS-based studies of Gurushidze & al. 2008 presented disproof of this hypothesis, but detected that most large sections were non-natural conglomerates of distantly related subunits. This phylogenetic structure was confirmed by sequences of the *trn*L-*trn*F region of chloroplast DNA (Gurushidze & al. 2010). The resulting more specified classification reflecting the natural relationships within subg. *Melanocrommyum* was established by Fritsch & al. 2010 (see above). However, not even this final study of ITS sequences could resolve the phylogenetic relationship of all infra-subgeneric groups. As soon as a more suitable molecular marker system will be available, a re-evaluation of a broad taxonomic sampling will be essential, if possible with addition of hitherto missing or poorly represented species.

DNA contents. Ohri & al. 1998 found rather uniform and moderately high DNA values in a range of 40–50 pg 2C DNA content per nucleus although a few taxa had only about 30 pg. A much more comprehensive investigation of Gurushidze & al. 2012 measured a range from 26–60 pg with most common data ranging from 33–46 pg referred to diploid level. This analysis showed significant differences in DNA content among phylogenetic clades, while closely related taxa showed highly similar genome size values. Estimation of ancestral genome sizes revealed lineages with increasing as well as decreasing DNA content. Thus the conclusion of Friesen & al. 2006, that phylogenetically derived groups of the genus *Allium* have lower DNA content than more ancient ones, is not valid for subg. *Melanocrommyum*.

Phylogenesis. Although primary evolution may have happened in the old Central Asian mountain systems of Tienshan and Alai, the diversification and rapid speciation surely took place during the late Tertiary phase, when enormous regions on the Northern Hemisphere became dryer and, thus, could be newly colonized by drought adapted taxa. Like in subg.

Allium, there are several complexes in which species limits are rather diffuse, indicating a young phylogenetic state (Hanelt & al. 1992).

Application of a statistical dispersal-vicariance analysis to molecular markers (ITS and chloroplast DNA *rps16*intron; Li & al. 2010) to the second evolutionary lineage of *Allium* indicated that the ancestor of the subgenera *Porphyroprason*, *Vvedenskya* and *Melanocrommyum* originated in eastern Asia, then dispersed to Central Asia along the north coast of the Tethys sea, where subg. *Melanocrommyum* quickly colonized the territories of the former Tethys sea and radiated in Central Asia. The resulting taxa expanded their ranges via dispersal into other areas such as western Asia and the Mediterranean and diversified in these regions. Later also other dispersal events occurred in reverse and in other directions.

An attempt to draw the phylogenetic history of subg. *Melanocrommyum* from molecular markers of chloroplast DNA is under progress but has not been finished yet.

7. Economical Importance

A remarkable number of species own olfactory and taste qualities more or less similar to cultivated species like common onion, garlic, rakkyo, leek, etc. belonging to other subgenera. Therefore it is not surprising that leaves and bulbs (rarely whole plants) of about 30 species of subg. *Melanocrommyum* were reportedly collected in the wild by local people and applied as spices, vegetables, and medicinal plants (Kochkareva & Chukavina 1985, Khassanov & Umarov 1988, Keusgen & al. 2006, Keusgen & Fritsch 2008). Also some attempts to cultivate excessively collected taxa were reported (Hanelt 2001).

Rather many *Allium* species possess a striking ornamental habit caused by multiflowered inflorescences in different conspicuous colors and spectacular foliage. Some are forming dense patches with short floral stems, others grow as grand single plants or in loose groups with large flower heads on eminent scapes. Already more than 100 years ago the first members of subg. *Melanocrommyum* were introduced in European gardens. They have become popular for rock gardens, herbaceous beds and perennial borders, and even as cut flowers and for forcing. At the beginning of the 21st century the bulbs of about 25 species and a permanently growing number of selections and hybrid strains were regularly commercially offered, most of them multiplied by commercial producers of ornamental *Allium* bulbs (Intern. Checklist 1991, Kamenetsky & Fritsch 2002). Because plant enthusiasts and commercial growers of rare bulbs offer a much broader assortment of ornamental members of subg. *Melanocrommyum*, the number of cultivated ornamentals will considerably rise in the future.

8. Key

8.1 Remarks

Many living *Allium* specimens cannot be reliably determined applying the descriptions presented by floras – the characters used in keys and descriptions were obviously deduced from herbarium specimens which are known to have generally lost many characters during drying. Therefore this new key was developed in many steps over a longer period condensing the experiences of many years of observations during fieldwork and investigation of cultivated specimens. Repeatedly some characters or character states of living plants from type locations differed from those given in the original descriptions and the floras. Thus not only hitherto unrecognized characters could be added, also some corrections were included. Regrettably, only about 120 out of the roughly 170 species and subspecies belonging to subg. *Melanocrommyum* (see chapter 9) could up to now be studied as living plants. Therefore the characters of these unstudied taxa had to be copied from descriptions and floras and remained necessarily incomplete and may contain mistakes. Because a comprehensive electronic storage of data and detailed photographs began only in the early 1990ies, the results of the earlier decade of investigations were scarce and were complemented by a rather meager photographic documentation. Thus also the knowledge of some taxa studied only during that time remained fragmentary. Also under this respect the key is incomplete and may contain errors.

Molecular data (Fritsch & al. 2010) indicated an inhomogeneous structure of several groups accepted in the conspectus (chapter 9), and other taxa were only preliminary affiliated. On the other hand, some molecularly homogeneous sections comprise taxa remarkably differing by some morphological features. Thus the members of several sections and subsections can be reached on different ways, and the key decisions remain unclear when the characters requested are not available or cannot well be seen.

Rather many morphological characters of *Allium* plants may vary remarkably depending on environmental conditions. It was intended to mention a reasonable amount of variation seen during fieldwork and under cultivation, but these measures may differ from those taken at other places. Such influences should be taken in account when using the key.

It was intended to give clear alternatives in the bifurcations. When a group is keyed out and the alternative leads ahead in the key, sometimes (an) additional character(s) supplement the main key characters to enable a clearer decision. These additional characters are no key characters.

Allium oreophilum C. A. Mey., the only species of subg. *Porphyroprason*, is morphologically very similar to species of subg. *Melano-*

crommyum (where it was formerly included). Therefore it was added to the key.

Numbers in square brackets at the end of the group names refer to the group numbers of the conspectus (chapter 9).

8.2. Illustrated Key to the Sections and Subsections of subg. *Melanocrommyum* for Living Plants

1\. Flowers narrowly campanulate or narrowly funnel-shaped, filaments basally connate, 1/4–3/4 as long as tepals which are basally to 1/4–1/3 of their length connate; inflorescences with rarely more than 100 flowers, initially sometimes very dense but after anthesis commonly lax 2

1* Flowers cup-shaped, widely funnel-shaped, or in different modes star-like, tepals basally not or very shortly connate, filaments shorter or longer than tepals; inflorescences divers 5

2\. Tepals crème or whitish, purple towards the tip, margin of inner tepals finely undulate-denticulate; inflorescences globose; ripe capsules dropping from receptacle (*Allium gypsaceum*) sect. *Popovia* [17]

2* Tepals ± unicolored, margin of tepals even, flowers often with a sweetish odor like hyacinths; inflorescences fasciculate; ripe capsules not dropping sect. *Regeloprason* 3

3\. Pedicels permanently elongating during anthesis and afterwards for 3–10 times, thus infructescences very loose in the fruiting stage; leaf laminae mostly thick and fleshy, patent or adpressed to soil 4

3* Pedicels elongate no more than twice during anthesis and afterwards; flowers intensely sweet scented somewhat like hyacinths; leaf laminae thin, straight or obliquely upright positioned subsect. *Odoratae* [3.3]

4\. Infructescences ± semiglobose (if ovate: *A. lipskyanum*) and very loose with thin pedicels subsect. *Diffusoumbellata* [3.2]

4* Infructescences ± umbel-like, less loose with thick pedicels, often with superposed parts
subsect. *Regeloprason* [3.1]

5. (1*) Scape above soil (1–)3–20 (rarely up to 40) cm long, straight, ascendent, or S-shaped flexuous 6

5* Scape 30–120 cm long (if somewhat shorter then ovaries shiny and purple to black at begin of anthesis), straight or somewhat flexuous 29

6. Scape subcylindrical, weakest and thinnest at the tip; inflorescences loose, often not much more than 100 flowers 7

6* Scape ± conical, thickest below inflorescence, basally narrow and weak and often only slightly lignified; inflorescences loose or dense 16

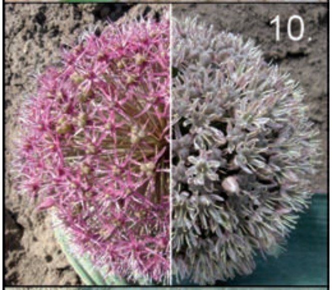
7. Scape ± flexuous; inflorescences globose; tepals ovate to elliptic, 8–13 mm long, after anthesis not much changing 8

7* Scape ± straight; inflorescences broadly fastigiate to semiglobose, after anthesis subglobose; tepals ovate and concave or lanceolate and claw-like inverted, after anthesis incurved or recurved, ± crumpled or spirally contorted; anthesis begins in the area near the top of the inflorescences 9

8. Tepals 2.5–4 mm broad, concave; ripe capsules dropping from receptacle; leaf laminae ovate to lanceolate
sect. *Thaumasioprason* [18]

8* Tepals 5–7 mm broad, in anthesis convex; anthesis begins near basal part of inflorescences; leaf laminae linear-lanceolate *Allium oreophilum*
(subg. Porphyroprason sect. *Porphyroprason)*

9. Leaves long-elliptic to ovate, 4–10 cm wide, initially violet-bluish with purple margin, finally deep-green, long-



itudinally sulcate; scape flexuous; ovaries depressed-globose 10

9* Leaves less than 3 cm wide, long-elliptic to narrowly lanceolate or linear, green or glaucous; ovaries depressed turbinate-pyriform, rarely depressed-globose 12

10. Tepals narrowly linear-lanceolate, pinkish, brownish or red, patent, plicate; ovary coarse, stipitate, green or reddish; tip of capsule with a deeply excised centre (*Allium karataviense*) sect. *Miniprason* [10]

10* Tepals broadly lanceolate to ovate, white or greenish; ovaries not stipitate, glossy (and black at the begin of the anthesis), or rugose and green 11

11. Ovaries smooth, shiny, blackish *Allium bisotunense* alliance [4.3]

11* Ovaries coarse, dull, green *Allium colchicifolium* alliance [4.5]

12. Flowers flat star-like, tepals patent, free near base, later reflexed and spirally contorted; filaments as long as tepals, straight, fleshy, subulate; scapes short and flexuous much shorter than leaves, rarely somewhat longer and straight; inflorescences ± hemispherical, rather dense; ovary stipitate and coarse sect. *Megaloprason* subsect. *Humilicognata* [9.2]

12* Flowers bowl-shaped to cup-like with ± incurved tepals, or broadly funnel-shaped with recurved tepals; filaments ± remarkably shorter than tepals 13

13. Tip of ovary with six horn-like outgrowths; leaf laminae narrowly lanceolate, 3–5 times as long as the (above soil) 1–3 cm long scape; tepals long-elliptic, straight after anthesis (*Allium hexaceras*) sect. *Acaule* [16]

13* Ovary without horn-like outgrowths; leaf laminae up to 2 times longer than the 5–20 cm long scape 14

14\. Leaves 1–3, laminae arched or screw-like recurved; inflorescences ± semiglobose to subglobose; tepals claw-like inverted or concave, after anthesis recurved and crumpled; ovary ± finely coarse, green with purple flush; capsule shortly obovate, ± angled sect. *Brevicaule* [20]

14* Leaves (3–)4–7, laminae linear to lanceolate, inflorescences initially fastigiate finally semiglobose, ovaries smooth, shiny, like filaments blackish-purple 15

15\. Steppe plants; scape 15–30 cm long, straight; flowers funnel-shaped, flesh-colored or white, stigma undivided *Allium noëanum* alliance [4.7]

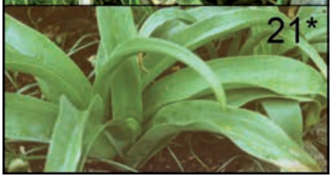
15* Desert plants; scape 10–20 cm long, flexuous; flowers bowl-shaped, tepals white with purplish back or deep purple, stigma tripartite *Allium rothii* alliance [4.9]

16\. (6*) Leaf lamina divided into long thread-like parts, much shorter than the scape; inflorescences always loose, umbel-like sect. *Verticillata* [12]

16* Leaf lamina ovate or lanceolate to linear, not lengthwise divided 17

17\. Leaves 1–2, laminae ± linear, lengthwise folded, as long as the flexuous and narrow (4–6 mm in diameter) scape; inflorescences subglobose, pedicels incurved, in anthesis unequally long; tepals concave, ovate (*Allium aroides*) sect. *Aroidea* [15]

17* Leaves (2–)4–8, mostly ovate, rarely linear or lanceolate, basally canaliculate, rarely more than 2 times longer than scape; scape often thicker than 8 mm below the inflorescences; tepals ligulate or long lanceolate to trian-



gular, in fruiting stage straight, sometimes hard and prickly 18

18. Flowers flat star-like, tepals straight or recurved, filaments whitish or (dark) purplish, basally united forming a cup separate from the tepals; ovaries pyriform (stipitate), dull and tuberculate (rarely smooth and shiny) sect. *Asteroprason* 19

18* Flowers broadly funnel-shaped star-like, rarely nearly ovoid, tepals straight or incurved 20

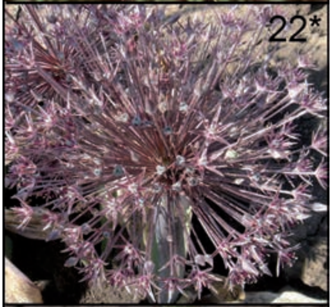
19. Plants compact, small; leaves glabrous; tepals longitudinally enrolled, crumpled, not prickly in the fruiting stage, filaments slightly darker than tepals subsect. *Asteroprason* [7.1]

19* Stature larger; leaves hairy or at least densely toothed along margins; tepals in fruiting stage stiff and prickly, filaments conspicuously darker than tepals subsect. *Christophiana* [7.2]

20. Scape obconical, the narrower base decomposing; inflorescences always loose with pedicels of unequal length; flowers ovoid or funnel-shaped, ovaries turbinate or depressed-pyriform, rarely depressed-globose, smooth and dull, filaments ± longer as tepals sect. *Kaloprason* 21

20* Scape indistinctly obconical, basally not decomposing; inflorescences (at least initially) dense, fasciculate to semiglobose, pedicels subequal; tepals very narrowly lanceolate up to triangular, recurved, in dry state stiff and sometimes prickly; filaments equal or shorter as tepals; ovary ± globose sect. *Acanthoprason* 23

21. Leaf laminae broadly lanceolate, canaliculate, always green; flowers ovate or star-like; ovaries ± turbinate or depressed-globose subsect. *Kaloprason* [19.1]



21* Leaf laminae ligulate-obovate and canaliculate or oblong and nearly plane, green or purple suffused; flowers star-like, tepals patent, ovaries depressed-pyriform 22

22. Leaf laminae always green, ligulate-obovate and canaliculate, not sulcate; tepals after anthesis irregularly contorted subsect. *Schubertia* [19.3]

22* Leaf laminae initially sulcate and purple suffused with purple margin, oblong and nearly plane; tepals after anthesis ± convolute, crumpled or erect and prickly subsect. *Ligulifolia* [19.2]

23. Filaments ± as long as the whitish, pale-purplish or flesh-colored tepals, tepals after anthesis stiff and prickle-like *Allium materculae* alliance [5.5]

23* Filaments up to 1/2 as long as the white, pink or purple tepals becoming stiff but not prickly after anthesis 24

24. Filaments single-colored, or base slightly darker than tip 25

24* Tip of filaments remarkably darker than the other parts 27

25. Tepals linear-triangular to lanceolate, 12–18 mm long, 1.5–2(–2.5) mm wide; filaments 1/5–1/3 as long as tepals *Allium haemanthoides* alliance [5.4]

25* Tepals widely lanceolate or ovate-obtuse, up to 12 mm long, filaments 1/3–1/2 as long as tepals 26

26. Tepals ovate-obtuse, pink to purplish; filaments 1/3 of tepal length and whitish throughout or pinkish near the very base, nearly touching one another with the margin above base *Allium akaka* alliance [5.1]

26* Tepals widely lanceolate to subovate, filaments 1/3–1/2 as long and as dark as the tepals; margins of filaments

above base with some distance to one another
Allium ubipetrense alliance [5.7]

27. Ovary smooth and glossy with six radial bulges at the tip; tepals green or purple-brown; filaments purple, base much paler and bowl-shaped connate
Allium minutiflorum alliance [5.6]

27* Ovary dull and ± coarse; tepals whitish, pinkish, or lilac 28

28. Leaves (broadly) lanceolate, obliquely upwards directed, only basally canaliculate, above even and hanging down; tepals acute, triangular up to narrowly lanceolate
Allium austroiranicum alliance [5.2]

28* Leaves ± linear or narrowly lanceolate, spread ± parallel to the soil, throughout canaliculate; tepals lanceolate to linear-ovate, subacute or obtuse
Allium derderianum alliance [5.3]

29. (5*) Nectaries mounding as a pocket-like cave in the lower third of the ovary; scape always smooth and dull; inflorescences always dense; ovaries always stipitate and rough 30

29* Nectaries mounding as an inconspicuous pit or short slit near the base of the ovary; scape, inflorescences, and ovaries variously shaped 31

30. Scape 60–100 cm long, leaves 3–4, laminae long elliptical; inflorescences subglobose or subellipsoidal with flat base; pedicels straight, stiff, and thickish; tepals lanceolate, in anthesis patent; dilatated base of all filaments without teeth; ovary long stipitate with rugose surface
sect. *Decipienta* [2]

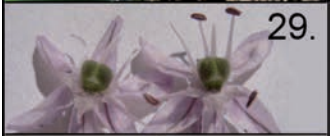
30* Scape up to 60(–80) cm long; leaves 2–3(–5), laminae linear-lanceolate; in-


26*


27.


28.


28*


29.


30.

florescences depressed-globose, pedicels bent upwards; tepals long triangular, in anthesis turned backwards but upper part slightly inverted; dilatated base of inner fila-ments with two or more teeth; ovary substipitate, pyriform-triangulate, finely tuberculate
sect. *Longibidentata* [1]

31. Scape during anthesis longer than about 100 cm 32

31* Scape during anthesis not so tall 37

32. Flowers white, tepals narrowly lanceolate or triangular 33

32* Flowers lilac to pinkish-purple, tepals oblong to lanceolate 34

33. Tepals triangular; leaf laminae oblong with smooth margins, 4–10 cm broad (*Allium backhousianum*)
sect. *Acmopetala* subsect. *Acmopetala* [11.1]

33* Tepals narrowly linear, leaf laminae linear-lanceolate with coarse margins, 2–4 cm broad (*Allium zergericum*)
sect. *Acmopetala* subsect. *Acmopetala* [11.1]

34. Leaf laminae linear-lanceolate, 1.5–3 cm broad, scape smooth or ribbed 35

34* Leaf laminae oblong to broadly lanceolate, 3–10 cm wide, scape always smooth 36

35. Leaf number 6–12, laminae with smooth margins; scape ribbed; tepals lanceolate-triangular, tip with median vein (*Allium rosenorum*)
sect. *Procerallium* subsect. *Costatae* [14.2]

35* Leaf number 2–4, laminae with very coarse basal margins; scape smooth; tepals ovate-lanceolate, tip without median vein (*Allium tschimganicum*)
sect. *Acmopetala* subsect. *Pharmakoprason* [11.5]

36\. Scape shiny, leaf laminae often hairy or toothed along margin; capsules not dropping sect. *Procerallium* subsect. *Elatae* [14.1]

36* Scape dull; leaves smooth with smooth margins; ripe capsules dropping from receptacle (*Allium giganteum*) sect. *Compactoprason* [13]

37\. Ovaries ± globose with 6 narrow furrows, not stalked, at begin of anthesis at least partly ± black, smooth, ± shiny, surface cells not convex 38

37* Ovaries depressed-globose triangular (with 3 narrow and 3 wide furrows), during whole anthesis green, surface more or less rough, dull, surface cells distinctly convex to tuberculate 41

38\. Leaf laminae broadly lanceolate or long-elliptic to ovate, shorter than the 30–80 cm long scape; tepals patent 39

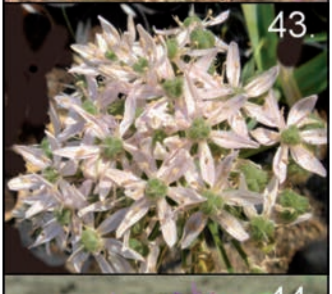
38* Leaf laminae narrowly linear to lanceolate, scape 20–40(–60) cm long; tepals directed to the side or soon recurved 40

39\. Scape 40–90 cm long, straight; leaf laminae broadly lanceolate, not undulate, shorter than scape; tepals obtuse, elliptic and white to pink or narrowly-elliptic and blackish-purple *Allium multibulbosum* alliance [4.6]

39* Scape 20–50 cm long, flexuous, leaf laminae long-elliptic to ovate, widely undulate; tepals elliptic, obtuse, white to pink *Allium orientale* alliance [4.8]

40\. Leaf laminae linear-lanceolate, as long as scape; tepals long-elliptic, white *Allium asclepiadeum* alliance [4.2]

40* Leaf laminae narrowly lanceolate, half as long to as long as the scape; tepals blackish-purple (rarely pinkish) *Allium cardiostemon* alliance [4.4]



41. (37*) Inflorescences (sub)globose, very dense (up to 3000 flowers) with thin pedicels of unequal length; capsules depressed-globose three-sided, finally opening with three narrow fissures and dropping down from the receptacle sect. *Compactoprason* 42

41* Inflorescences fastigiate to globose, moderately dense also in fruiting stage with pedicels of subequal length and not dropping from receptacle, capsules obconical or ovoid, locules ± widely opening 43

42. Tepals erect after anthesis, capsules with one seed per locule (but often irregularly shaped and only one seed per capsule) subsect. *Erectopetala* [13.1]

42* Tepals reflexed and spirally enrolled after anthesis; capsules open rather widely and contain commonly two seeds per locule (*Allium majus*) subsect. *Spiralopetala* [13.3]

43. Inflorescences fastigiate to semiglobose; seeds nearly flat and coarsely sharp-edged, 4–5 mm long; leaf laminae linear-lanceolate, shorter than scape; tepals long-elliptic, obtuse, acutish, patent, rose; ovaries dull, green, coarse, three-sided globose *Allium nigrum* alliance [4.1]

43* Inflorescences semiglobose or subglobose to globose; seeds subglobose, reticulate-rugose, shorter than 4 mm 44

44. Leaf laminae broadly lanceolate, sulcate, violetish-green; inflorescences semi- or subglobose, capsules long-ovoid (*Allium komarowii*) sect. *Compactoprason* subsect. *Komaroviana* [13.2]

44* Leaf laminae variously shaped, without conspicuous furrows, often glaucous but not violetish-green; inflorescences ± globose 45

45. Inflorescences dense, ± depressed-globose; tepals ovate to lanceolate, of straw-like consistence, at begin of anthesis three and later all reflexed, outer ones with up to four veins sect. *Pseudoprason* [6]

45* Inflorescences ± loose and globose; tepals narrowly lanceolate to triangular, soft, always one median vein only 46

46. Leaves 2–4, laminae narrowly linear-lanceolate; ovary finely tuberculate; capsules ovate-triangular; seeds rather flat drop-shaped, sharply and reticulately angled 47

46* Leaves (4–)5–8(–12), laminae narrow or broad, linear or lanceolate; ovary coarsely tuberculate; capsule broadly triangular-pyriform, widely opening; seeds thick, ovate to comma-shaped, rugose 51

47. Scapes 30–60 cm long, conical, widest below the moderately loose, depressed-globose inflorescences; flowers flat star-like, tepals narrowly linear-lanceolate, obtuse with narrow median vein, upper half of filaments recurved (*Allium taeniopetalum*) sect. *Stellata* [8]

47* Scapes commonly 30–80 cm long, ± cylindrical; inflorescences semi- to subglobose and finally longer than broad; flowers bowl-shaped star-like; tepals ± acute, median vein broadest in the upper part or not reaching the tip; capsules ± ovate, moderately wide opening; filaments oblique or straight sect. *Acmopetala* 48

48. Outermost leaf (without lamina) rough or with prominent ribs, dull, during anthesis still present subsect. *Durovaginata* [11.3]

48* Outermost leaf (without lamina) smooth, shiny, quickly decaying 49

49. Median vein widest and thickest in the upper half of the spoon-shaped tepals; scape 30–60(–90) cm long, cylindrical, smooth; leaf laminae linear-lanceolate, dull or glossy, up to 4.5 cm wide
subsect. *Inornatae* [11.4]
incl. subsect. *Albidiflora* [11.2]

49* Median vein ± narrow, often missing in the upper half of the ovate to triangular tepals; scape 50–120 cm long; leaf laminae never glossy, sometimes much wider 50

50. Scape always smooth; leaf laminae linear-lanceolate, up to 3 cm wide, containing a red sap; inflorescences semiglobose-conical, dense, finally longer than wide; tepals obliquely patent, acutely lanceolate-triangular, pink (*Allium tschimganicum*)
subsect. *Pharmakoprason* [11.5]

50* Scape smooth or basally ribbed; leaf laminae narrow linear to broadly lanceolate, 2–13 cm wide, sometimes hairy, only exceptionally with red sap; inflorescences semiglobose to globose; tepals obtuse (if long-acute then margins irregularely dentate), white or lilac to pink
subsect. *Acmopetala* [11.1]

51. (46*) Tepals ± narrowly lanceolate; scape smooth and glossy or (often only in the basal part) longitudinally ribbed and dull, 30–100(–150) cm long; ovary stipitate, tuberculate
sect. *Procerallium* 52

51* Tepals lanceolate, upper part longitudinally folded and therefore the ± obtuse tip seemingly acute; scape smooth and dull, (5–)40–80 cm long, ovary ± stipitate, coarsely tuberculate or smooth and glossy
sect. *Megaloprason* s. strictiss. 53

52. Scape at least in its lower part lengthwise prominently ribbed, 30–

80(–120) cm long; leaf laminae up to 3.5(–5) cm wide, never pubescent subsect. *Costatae* [14.2]

52* Scape smooth (but ribbed when dry), (50–)80–120(–150) cm long; leaf laminae up to 8(–12) cm broad, sometimes pubescent subsect. *Elatae* [14.1]

53. Basal part of leaf laminae distinctly petiole-like narrowed; tepals inconspicuously silvery-pinkish subsect. *Megaloprason* [9.1]

53* Basal part of leaf laminae narrowed but not petiole-like; tepals more intensely lilac to carmine colored 54

54. Bulb tunics papery, neither elongated in a neck nor splitting into fibers; margins of leaf laminae basally overlapping and collar-like outside bent; upper part of the papillate ovary with oblique-upwards directed and radially elongated outgrowths (*Allium sarawschanicum*) subsect. *Keratoprason* [9.3]

54* Bulb tunics firm, elongated into spirally twisted fibers along the bulb neck, base of the linear-lanceolate leaf laminae with parallel margins; ovaries glossy, smooth or with convex epidermis cell walls subsect. *Spiralitunicata* [9.4]

8.3. Explanation of the Figures

The numbers inside the single pictures refer to the numbers of the paragraphs of the key. Where no species names are mentioned in the paragraphs, the taxonomic affiliation of the photographs is as follows:

Fig. 1.: *Allium darwasicum* REGEL
Fig. 3.: *Allium lipskyanum* VVED.
Fig. 3*: *Allium darwasicum* REGEL
Fig. 4.: *Allium cupuliferum* REGEL
Fig. 4*: *Allium regelii* TRAUTV.
Fig. 8.: *Allium mirum* WENDELBO
Fig. 9*: *Allium caspium* (PALL.) M. BIEB. subsp. *caspium*
Fig. 11.: *Allium bisotunense* R. M. FRITSCH
Fig. 11*: *Allium moderense* R. M. FRITSCH
Fig. 12.: *Allium scotostemon* WENDELBO
Fig. 14.: *Allium eugenii* VVED.
Fig. 15.: *Allium noëanum* REUT. ex REGEL
Fig. 16. (above + below): *Allium verticillatum* REGEL
Fig. 19.: *Allium elburzense* WENDELBO
Fig. 19*: *Allium cristophii* TRAUTV.
Fig. 21.: *Allium caspium* (PALL.) M. BIEB. subsp. *caspium*
Fig. 21*: *Allium schubertii* ZUCC.
Fig. 22.: *Allium schubertii* ZUCC.
Fig. 22*: *Allium alexeianum* REGEL
Fig. 23.: *Allium graveolens* (R. M. FRITSCH) R. M. FRITSCH
Fig. 25.: *Allium haemanthoides* BOISS. & REUT. ex REGEL, s.str.
Fig. 26.: *Allium akaka* S.G. GMEL. ex SCHULT. & SCHULT. f. s. str.
Fig. 26*: *Allium ubipetrense* R. M. FRITSCH
Fig. 27.: *Allium chlorotepalum* R. M. FRITSCH & M. JAEGER
Fig. 28: *Allium austroiranicum* R. M. FRITSCH
Fig. 28*: *Allium egorovae* M.V. AGAB. & OGAN.
Fig. 29.: *Allium decipiens* FISCHER ex SCHULT. & SCHULT. f. subsp. *quercetorum* Seregin
Fig. 30.: *Allium decipiens* subsp. *quercetorum*
Fig. 30*: *Allium fetisowii* REGEL
Fig. 36: *Allium stipitatum* REGEL
Fig. 39.: *Allium multibulbosum* JACQ.
Fig. 39*: *Allium orientale* BOISS.
Fig. 40.: *Allium saralicum* R. M. FRITSCH
Fig. 40*: *Allium cardiostemon* FISCH. & C. A. MEY.
Fig. 41*: *Allium stipitatum* REGEL
Fig. 42.: *Allium macleanii* BAKER
Fig. 43.: *Allium nigrum* L. s. str.
Fig. 45.: *Allium koelzii* (WENDELBO) K. PERSS. & WENDELBO
Fig. 46*: *Allium stipitatum* REGEL
Fig. 48. left: *Allium costatovaginatum* KAMELIN & LEVICHEV
Fig. 48. right: *Allium severtzovioides* R. M. FRITSCH
Fig. 48*: *Allium sewerzowii* REGEL
Fig. 49.: *Allium sewerzowii* REGEL

Fig. 50*: *Allium vvedenskyanum* PAVLOV
Fig. 51*: *Allium rosenbachianum* REGEL
Fig. 52. left + right: *Allium rosenorum* R. M. FRITSCH
Fig. 52* left + right: *Allium stipitatum* REGEL
Fig. 53.: *Allium rosenbachianum* REGEL
Fig. 54* left + right: *Allium suworowii* REGEL

9. Updated Conspectus of *Allium* subg. *Melanocrommyum* (based on FRITSCH & al. 2010)

1. sect. *Longibidentata* (R. M. FRITSCH) R. M. FRITSCH – Type: *A. fetisowii* REGEL (2 species)
2. sect. *Decipientia* (OMELCZUK) R. M. FRITSCH – Type: *A. decipiens* FISCH. ex SCHULT. & SCHULT. f. (9 species and subspecies)
3. sect. *Regeloprason* WENDELBO – Type: *A. regelii* TRAUTV.
    - 3.1 subsect. *Regeloprason* (WENDELBO) KAMELIN s. str. – Type: *A. regelii* TRAUTV. (2 species)
    - 3.2 subsect. *Diffusoumbellata* R. M. FRITSCH – Type: *A. cupuliferum* REGEL (7 species and subspecies)
    - 3.3 subsect. *Odoratae* R. M. FRITSCH – Type: *A. darwasicum* REGEL (8 species)
4. sect. *Melanocrommyum* WEBB & BERTHEL. s. str. – Type: *A. nigrum* L.
    - 4.1 *Allium nigrum* alliance (2 species)
    - 4.2 *Allium asclepiadeum* alliance (10 species + *Allium mozaffarianii* MAROOFI & R. M. FRITSCH, *Allium meronense* FRAGMAN & R. M. FRITSCH)
    - 4.3 *Allium bisotunense* alliance (2 species; *A. keusgenii* R. M. FRITSCH became a synonym of *A. straussii* BORNM.)
    - 4.4 *Allium cardiostemon* alliance (3 species)
    - 4.5 *Allium colchicifolium* alliance (4 species)
    - 4.6 *Allium multibulbosum* alliance (5 species + *Allium basalticum* FRAGMAN & R. M. FRITSCH)
    - 4.7 *Allium noëanum* alliance (2 species)
    - 4.8 *Allium orientale* alliance (8 species + *Allium melanogyne* GREUTER, *Allium israeliticum* FRAGMAN & R. M. FRITSCH)
    - 4.9 *Allium rothii* alliance (2 species)
5. sect. *Acanthoprason* WENDELBO – Type: *A. akaka* S. G. GMELIN ex SCHULT. & SCHULT. f.
    - 5.1 *Allium akaka* alliance (1 species + *Allium mahneshanense* RAZYFARD, ZARRE & R. M. FRITSCH)
    - 5.2 *Allium austroiranicum* alliance (2 species + *Allium subakaka* RAZYFARD & ZARRE)
    - 5.3 *Allium derderianum* alliance (6 species + *Allium alamutense* RAZYFARD, ZARRE & R. M. FRITSCH, *Allium kurdistanicum* MAROOFI & R. M. FRITSCH)
    - 5.4 *Allium haemanthoides* alliance (2 species)
    - 5.5 *Allium materculae* alliance (2 species)
    - 5.6 *Allium minutiflorum* alliance (2 species + *Allium chlorotepalum* R. M. FRITSCH & M. JAEGER)
    - 5.7 *Allium ubipetrense* alliance (1 species)

6. sect. *Pseudoprason* (WENDELBO) K. PERSS. & WENDELBO – Type: *A. koelzii* (WENDELBO) K. PERSS. & WENDELBO (2 species)
7. sect. *Asteroprason* R. M. FRITSCH – Type: *A. elburzense* WENDELBO
    - 7.1 subsect. *Asteroprason* R. M. FRITSCH – Type: *A. elburzense* WENDELBO (5 species)
    - 7.2 subsect. *Christophiana* TSCHOLOK. – Type: *A. cristophii* TRAUTV. (2 species)
8. sect. *Stellata* (F. O. KHASS. & R. M. FRITSCH) R. M. FRITSCH – Type: *A. taeniopetalum* POPOV & VVED. (1 species, 3 subspecies)
9. sect. *Megaloprason* WENDELBO s. str. – Type: *A. rosenbachianum* REGEL
    - 9.1 subsect. *Megaloprason* R. M. FRITSCH s. str. – Type: *A. rosenbachianum* REGEL (4 species)
    - 9.2 subsect. *Humilicognata* R. M. FRITSCH – Type: *A. brachyscapum* VVED. (3 species)
    - 9.3 subsect. *Keratoprason* R. M. FRITSCH – Type: *A. sarawschanicum* REGEL (1 species)
    - 9.4 subsect. *Spiralitunicata* R. M. FRITSCH – Type: *A. suworowii* REGEL (2 species)
10. sect. *Miniprason* R. M. FRITSCH – Type: *A. karataviense* REGEL (1 species)
11. sect. *Acmopetala* R. M. FRITSCH – Type: *A. backhousianum* REGEL
    - 11.1 subsect. *Acmopetala* R. M. FRITSCH – Type: *A. backhousianum* REGEL (12 species)
    - 11.2 subsect. *Albidiflora* R. M. FRITSCH – Type: *A. saposhnikovii* NIKITINA (1 species)
    - 11.3 subsect. *Durovaginata* R. M. FRITSCH – Type: *A. costatovaginatum* KAMELIN & LEVICHEV (4 species)
    - 11.4 subsect. *Inornatae* R. M. FRITSCH – Type: *A. sewerzowii* REGEL s. str. (2 species)
    - 11.5 subsect. *Pharmakoprason* R. M. FRITSCH – Type: *A. tschimganicum* O. FEDTSCH. s. str. (1 species)
12. sect. *Verticillata* KAMELIN – Type: *A. verticillatum* REGEL (2 species)
13. sect. *Compactoprason* R. M. FRITSCH – Type: *A. giganteum* REGEL
    - 13.1 subsect. *Erectopetala* F. O. KHASS. – Type: *A. giganteum* REGEL (4 species)
    - 13.2 subsect. *Komaroviana* F. O. KHASS. & R. M. FRITSCH – Type: *A. komarowii* LIPSKY (1 species)
    - 13.3 subsect. *Spiralopetala* F. O. KHASS. & R. M. FRITSCH – Type: *A. majus* VVED. (1 species)
14. sect. *Procerallium* R. M. FRITSCH – Type: *A. stipitatum* REGEL
    - 14.1 subsect. *Elatae* R. M. FRITSCH – Type: *A. stipitatum* REGEL (3 species)
    - 14.2 subsect. *Costatae* R. M. FRITSCH – Type: *A. jesdianum* BOISS. & BUHSE (7 species and subspecies + *Allium oriento-iranicum* NESHATI, ZARRE & R. M. FRITSCH)
15. sect. *Aroidea* F. O. KHASS. & R. M. FRITSCH – Type: *A. aroides* POPOV & VVED. (1 species)
16. sect. *Acaule* R. M. FRITSCH – Type: *A. hexaceras* VVED. (1 species)
17. sect. *Popovia* F. O. KHASS. & R. M. FRITSCH – Type: *A. gypsaceum* POPOV & VVED. (1 species)

18. sect. *Thaumasioprason* Wendelbo – Type: *A. mirum* Wendelbo (4 species)
19. sect. *Kaloprason* K. Koch – Type: *A. caspium* (Pall.) M. Bieb.
    - 19.1 subsect. *Kaloprason* (K. Koch) Kamelin s. str. – Type: *A. caspium* (Pall.) M. Bieb. (3 species and subspecies)
    - 19.2 subsect. *Ligulifolia* R. M. Fritsch – Type: *A. alexeianum* Regel s. str. (4 species)
    - 19.3 subsect. *Schubertia* Kamelin – Type: *A. schubertii* Zucc. s. str. (1 species)
20. sect. *Brevicaule* R. M. Fritsch – Type: *A. sergii* Vved. (3 species)
21. Species incertae sedis (4 species)

Altogether 169 species and subspecies are accepted. Complete citations of all species and subspecies are presented online (<http://apps.kew.org/wcsp/home.do>, <http://www.ipni.org/ipni/plantnamesearchpage.do>). Ongoing revisional work in Asia Minor, Southwest Asia, and Central Asia will certainly result in the description of some new species and subspecies in the future.

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